SYSTEMATICS, PHYLOGENY AND EVOLUTION OF DIETES (IRIDACEAE)¹

PETER GOLDBLATT²

ABSTRACT

Dietes is a member of Iridaceae-Iridoideae and is probably the most primitive member of the Old World tribe Irideae. It shares characteristics of both *Iris* and the African genus *Moraea* and is most likely close to the ancestral stock that gave rise to these more specialized genera. Dietes comprises six species, five African and one remarkable disjunct on Lord Howe Island between Australia and New Zealand, D. robinsoniana. The South African D. bicolor appears more closely related to D. robinsoniana than to the other African species, and these two share several characters primitive in the genus. The remaining four African species include the wide-ranging D. iridioides, which extends from the southern Cape to Ethiopia, and three more localized eastern southern African species.

Dietes is a small genus of Iridaceae, closely allied to the African genus Moraea and to the widespread Northern Hemisphere genus Iris. Six species are currently recognized, five African and one restricted to Lord Lowe Island in the Tasman Sea between Australia and New Zealand (Fig. 1). In spite of the extraordinary disjunction in the distribution, there seems no doubt that Dietes is a natural genus, all the species sharing unique vegetative and floral structures and a basic chromosome number of x = 10.

HISTORY

The name *Dietes* was first proposed by R. A. Salisbury in 1812, but as published it was nomenclaturally invalid, lacking description or reference to a previously published generic description. Salisbury chose the name *Dietes* to indicate what he believed to be its dual affinities to both *Iris* and *Moraea*, a point of view fully supported here. Few authors accepted the genus initially, though Sweet (1830, 1839) put forward several combinations, unfortunately never validating the genus with a description. *Dietes* appears again in the literature in 1846 in an article by Spae concerning the species currently called *D. bicolor*. Spae used both *Moraea bicolor* and *Dietes bicolor* in the title, but apparently regarded *Moraea* as the correct generic name. Later, in 1852 when Spae again wrote about *D. bicolor*, he unambiguously placed it in *Moraea*.

Dietes was only fully accepted in 1866 by Klatt, who provided a complete generic description. Klatt acknowledged Salisbury as the source of the name and recognized three species in the genus, D. bicolor, D. catenulata, and D. compressa. The last two are, in my opinion, the same species and conspecific with the much earlier D. iridioides. It was also Klatt who realized that the newly described Australasian species Iris robinsoniana F. Muell. belonged in Dietes (Klatt, 1882).

² B. A. Krukoff, Curator of African Botany, Missouri Botanical Garden, Post Office Box 299, St. Louis, Missouri 63166.

¹ This research was supported by grant DEB 78-10655 from the U.S. National Science Foundation. I thank Mrs. A. A. Mauve-Obermeyer for her helpful suggestions and collaboration in this project and Margo Branch for preparation of the illustrations.

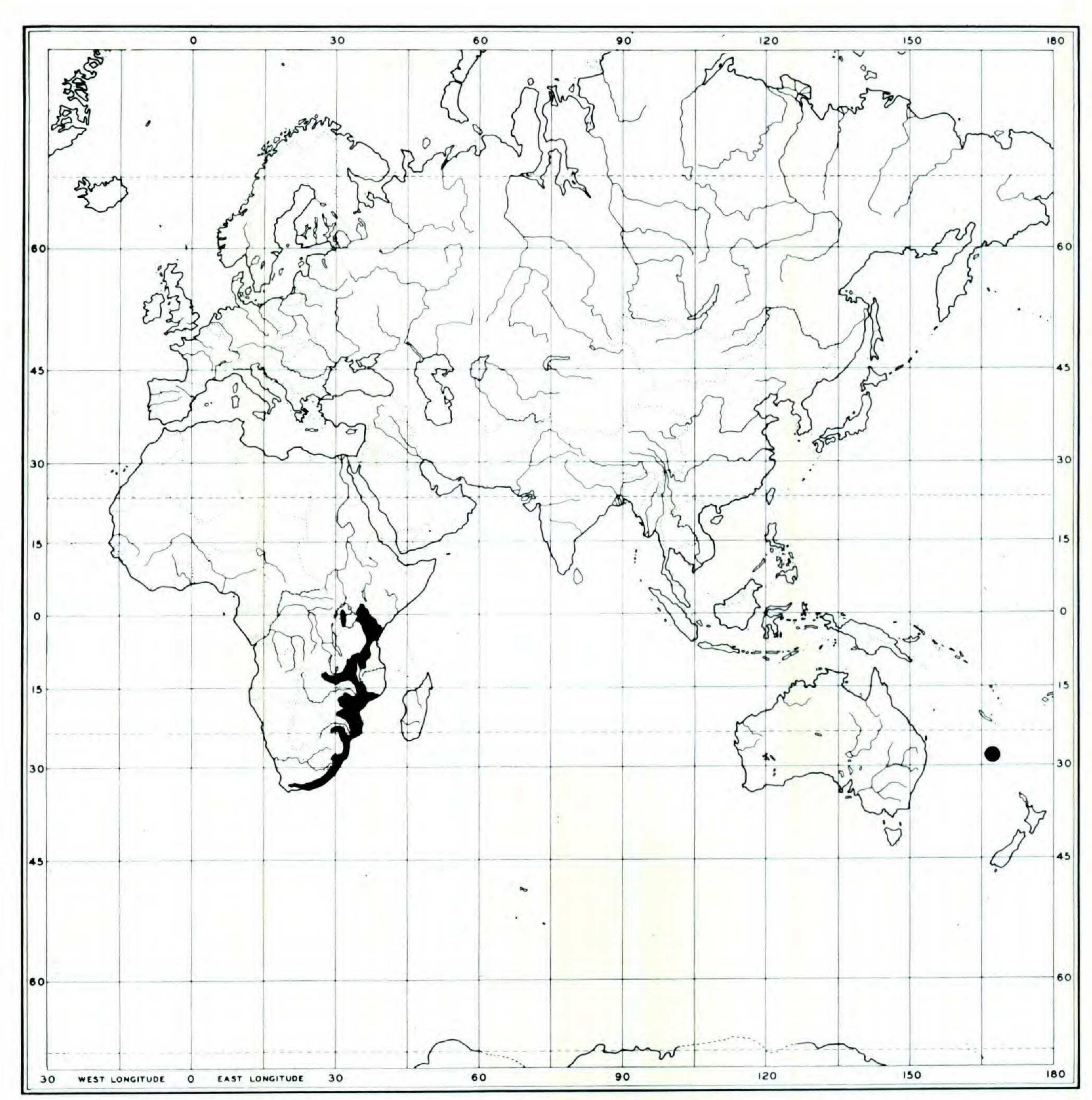


FIGURE 1. Worldwide range of *Dietes*, showing the distribution of the five African species in southern and eastern Africa and the single species on Lord Howe Island.

Salisbury was not the first to consider *Dietes* a distinct genus. Medikus in 1790 published *Naron* which, though confusingly described, is clearly a new genus accommodating only the Linnaean species *Moraea iridioides*, although under the superfluous name *N. orientale. Naron* was never accepted and apparently on only one occasion is the genus again mentioned, by Moench in 1794 where he proposed the corrected combination *N. iridiodeum* (L.) Moench. *Naron* was completely overlooked subsequently, although a perfectly valid earlier synonym for *Dietes*, even typified by the same species under a different name.

Dietes did not receive general acceptance during the nineteenth century, although Klatt (1882, 1895) continued to recognize the genus. Instead, J. G. Baker's view of Dietes as a subgenus of Moraea prevailed and the genus was so treated in the important works, Flora Capensis (Baker, 1896) and Flora of Tropical Africa (Baker, 1898). In 1928 Brown raised Dietes once more to generic rank,

and he described two new African species, *D. grandiflora* and *D. prolongata*, the latter now considered merely a minor variant of *D. iridioides*. From this time, *Dietes* was consistently recognized in southern Africa for the genus, as when Gerstner in 1943 described the Natal forest species *D. butcheriana*.

Brown (1928) was also responsible for changing the name of *D. iridioides* to *D. vegeta* based on *Moraea vegeta* L., a species dating from 1762 which he believed to be typified by the same figure that is the type of *M. irioides* L. (1767). As explained at length (Barnard & Goldblatt, 1975), this was incorrect. *Moraea vegeta* is in fact the type species of *Moraea* and is not a *Dietes*.

An important contribution to the understanding of *Dietes* was made by A. A. Obermeyer who, in a series of four beautifully illustrated articles in *Flowering Plants of Africa* (Obermeyer, 1967a, 1967b, 1968a, 1968b), reviewed current knowledge of *Dietes*. She contributed valuable new data on the biology of the genus based on her own observations and those of R. G. Strey, the Natal botanist. Obermeyer also described a new species, *D. flavida*, bringing the number of species in the genus to six.

Dietes is now widely known in many parts of the world as a horticultural subject. Although not the earliest name for the genus, Dietes is correct as it has been conserved against Naron (Goldblatt, 1973; Brummitt, 1978) in the interests of nomenclatural stability.

RELATIONSHIPS

Dietes is undoubtedly allied to both *Iris* and *Moraea*. Opinion has differed as to which of the two is more closely related, but there is perhaps a consensus that *Dietes* and *Moraea* are closer simply because both are Southern Hemisphere genera. I believe it may be closer to the truth to consider *Dietes* a primitive genus in the Iridioideae, and ancestral to *Moraea* and *Iris*. *Dietes* appears to me to have a combination of the more unspecialized features of both *Iris* and *Moraea*. It is an evergreen herb of areas with a fairly equable climate. It has a thick persistent rhizome, a fan of equitant, tough, long-lived leaves, and a freely branching scape which in *D. robinsoniana* and *D. bicolor* is paniclelike. The flower consists of free, spreading, clawed tepals; typically entirely free stamens (the filaments are joined basally in a form of *D. iridioides*); and flattened petaloid style branches each with the transverse stigmas and paired crests typical of both *Iris* and *Moraea*.

Iris differs in several respects: most species are deciduous; the inflorescence is usually reduced rather than freely branched; the perianth is usually united to form a tube; and the tepals are dimorphic with large pendant outer tepals and smaller, usually erect inner tepals. Important features shared with Dietes are: the rhizome, clearly primitive in Iris; the basically isobilateral leaf (specialized in some species and subgenera and square or bifacial); free stamens; and spathe valves free to base.

In *Moraea* the rootstock is always a corm, the leaf fundamentally bifacial (occasionally terete), and the deciduous condition is normal. In the flower, tepals may be subequal, but if so, both whorls are usually strongly reflexed (more often the inner tepals are smaller, sometimes erect, and occasionally lacking); a perianth tube is found in two species, but free tepals are basic to the genus; the

TABLE 1. Comparison of critical characteristics of Dietes, Iris, and Moraea.a

Character	Taxa		
	Dietes	Iris	Moraea
Evergreen	+	(+)-	
Rhizome	+	+(-)	
Free tepals	+		+(-)
Free stamens	+	+	
Free spathe valves	+	+	(+)-
Isobilateral leaf	+	+(-)	
Subequal tepals	+		+-

^a The unspecialized condition of each organ is listed with presence indicated by plus, absence by minus. Exceptions, usually derived, are in parentheses.

filaments are always contiguous at the base and with minor exceptions partially united; and the spathe valves of the majority of species are united at least in the lower part.

The similarities and differences between Dietes, Moraea, and Iris are summarized in Table 1, where it is evident that Iris and Dietes share more unspecialized (i.e., primitive) features than do Moraea and Dietes. It seems reasonable, therefore, to consider Dietes ancestral to Iris and to Moraea, with Moraea on balance probably having diverged somewhat farther than *Iris* from the ancestral type. On this line of reasoning, Dietes emerges as the basal genus of Old World Iridoideae and close to the ancestral stock which gave rise to Iris and its allies in the Northern Hemisphere (Hermodactylis, Belamcanda and Iris-segregate genera Iridodictyon, Juno, Xiphium, etc.) and to Ferraria, Moraea, and its cormiferous allies in Africa (Galaxia, Homeria, Hexaglottis, Gynandriris, etc.). In an earlier article in which I proposed this hypothesis (Goldblatt, 1976), I suggested a classification in which these Old World Iridoideae be grouped in a single tribe Irideae, subdivided as follows: Dietes, Iris, Hermodactylis, and Belamcanda be grouped in one subtribe Iridinae; the corm-bearing, bifacial leafed Moraea, Galaxia, Homeria, Hexaglottis, and Gynandriris be placed in another, Homeriinae Goldbl.; and Ferraria with an isobilateral leaf and a distinctive type of corm in a third, Ferrariinae Goldbl. It seems to me this treatment reasonably, though not perfectly, reflects what is known to date about the relationships of the genera of Old World Iridoideae.

Dietes exhibits some similarities with two New World iridoid genera, Neomarica and Trimezia. These genera also comprise evergreen, mainly forest species, and the rootstock in Neomarica is a creeping, persistent rhizome. Neomarica and Trimezia, as well as several other bulb-bearing New World Iridoideae, have flattened, rather petallike style branches, though usually narrower and smaller than those in the Old World Iridoidea. The New World genera differ consistently in one significant feature, the inner tepals, often elaborately folded, are nectiferous. In contrast, Old World species have flat inner tepals which rarely produce nectar, a function here of the outer tepals. It seems logical to group all New World Iridoideae in one tribe, the earliest name for which would seem to be Tigridieae.

TABLE 2. Chromosome numbers in Dietes. New counts are indicated in bold type.

Species	Diploid Number	Reference or Collection Data	
D. robinsoniana	20	Goldblatt (1979)	
D. bicolor	40	Goldblatt (1971); Chimphamba (1974)	
(as "Moraea iridioides var. bicolor")	40	Sharma & Sharma (1960)	
	40	Goldblatt 2884 (MO), South Africa, Cape, Kap R. valley.	
D. iridioides	20	Goldblatt 3732 (MO), South Africa, Cape, Swellendam distr.	
(as D. vegeta (L.) N.E.Br.)	20	Goldblatt (1971) (three localities)	
(as "Moraea iridioides var. johnsonii")	20	Sakai (1952); Sharma & Sharma (1960)	
(as "M. iridioides var. mcleyii")	40	Sharma & Sharma (1960)	
(as D. prolongata N.E.Br.)	20	Riley (1962)	
(as M. iridioides)	20	Banerjee & Sharma (1971)	
D. flavida	20	Admiraal s.n. (PRE), South Africa, Natal, Josini Dam.	
D. grandiflora	20	Goldblatt (1971); Chimphamba (1974)	
	20	Bayliss 7014 (MO), South Africa, Cape, Riebeek East.	
D. butcheriana	20	Goldblatt (1971)	

CYTOLOGY

Basic chromosome number in *Dietes* is x = 10 (Table 2). Four of the five African species are diploid, 2n = 20, while *D. bicolor* is tetraploid with 2n = 40 (Goldblatt, 1971; Chimphamba, 1974). *Dietes robinsoniana*, counted from unvouchered seed obtained from the Royal Botanic Gardens, Kew, also has 2n = 20, as does a hybrid *D. robinsoniana* \times *D. iridioides* raised by M. Boussard, Verdun, France (Goldblatt, 1979). Evidently, one of the named cultivars of *Dietes*, *D. iridioides* "mcleyii" is polyploid, 2n = 40 (Sharma & Sharma, 1960).

Karyotypes of all species are similar and comprise large metacentrics and submetacentrics and smaller acrocentrics. Size differences between matching pairs are small, and the range from largest to smallest is between 7 μ m and 4 μ m. Chromosome numbers in *Dietes* are listed in Table 2, which includes previously published data as well as the first report for *D. flavida*, and several original counts for species already known cytologically. Methods employed in obtaining counts have been described elsewhere (Goldblatt, 1978, 1979).

EVOLUTION

To summarize from the previous section, *Dietes* is seen as a primitive member of Iridoideae, and the most primitive genus of the Old World members of this subfamily. The species are all indigenous to equable habitats, either shady forest or forest margins, or along streams and other wet places. In Africa the genus is probably relatively ancient, probably dating back to Paleogene time, when the African climate was generally far more equable than it is at present. Extant species of *Dietes* are perhaps best viewed as relicts now restricted in distribution to well-watered habitats.

The single species on Lord Howe Island, which seems to be the most primitive in the genus, is clearly a relict, and is probably more like ancestral *Dietes* stock than is any living African species. Thus it probably has considerable antiquity on Lord Howe Island, a continental fragment that once had direct overland connections with Australia. It might be a relict of a once more widespread Australian group that has become extinct on the mainland. It is one of the puzzles of plant geography how *Dietes* reached Australasia, where it is the only member of the tribe Irideae. The most reasonable explanation seems to me long distance dispersal from Africa, probably well before the Pleistocene. In Paleogene time, when it seems likely that *Dietes* existed, Australia was well separated from Africa, but India occupied an intermediate position (Raven & Axelrod, 1974) and perhaps afforded a way-station for *Dietes*.

The evolution of *Iris* and its allies on the one hand and *Moraea* and its relatives on the other probably began in the mid-Oligocene as world climates began to deteriorate and habitats increased for strongly seasonal and deciduous forms like *Iris* and *Moraea*. The closure of the Tethys Sea in mid-Miocene time brought Africa-Arabia into contact with Eurasia, which would have greatly facilitated plant migration from Africa northward (Raven & Axelrod, 1978). It seems likely that the ancestors of *Iris* moved into Eurasia at about this time and began to spread and radiate from here throughout the Northern Hemisphere. By contrast, *Moraea* and its allies remained in Africa, sometimes growing near areas inhabited by *Dietes*, but always in drier habitats into which their dry-season dormancy allowed extensive radiation.

EVOLUTION AND SUBGENERIC RELATIONSHIPS

Within *Dietes* there seems to be one fundamental difference between the inflorescences of *D. robinsoniana* and *D. bicolor* compared with those of the remaining species. The inflorescence of *D. robinsoniana* with its much ramified paniclelike structure and large green bracts seems most likely to be closest to the ancestral and thus primitive type. *Dietes bicolor* is similar in inflorescence arrangement, but the plants and inflorescences are much smaller, the branching pattern more irregular, and the bracts smaller, and often dry. Occasionally branching may be suppressed in this species so that one or two upper nodes bear only a bract without an axillary branch.

The inflorescence of the other four species can in no way be called a panicle; the stem branches very irregularly, but bears several sheathing bracts along its upper length from the axils of which fertile branches, or stolons, may later be initiated. Occasionally stems may even be entirely unbranched, but sheathing bracts are always present indicating sites of suppressed, but potential, branching. It seems reasonable to consider this second type of inflorescence specialized by reduction from the panicle type in *D. robinsoniana* and *D. bicolor*.

A second character that unites D. robinsoniana and D. bicolor is the capsule which is similar in both, being globose in shape with a truncated, flat apex. The capsule of D. bicolor is much smaller, but in other respects very like that of D. robinsoniana. The capsules of the other species vary to some extent, but are generally elongated and tend to be oblong in shape. They seem more similar to

one another, despite differences in dehiscence, than to those of D. robinsoniana or D. bicolor.

It seems unreasonable to propose subgeneric divisions in so small a genus as *Dietes*, but it is important, I think, to emphasize the similarities between *D. robinsoniana* and *D. bicolor* relative to the other four species and to indicate their apparent primitive position in the genus. I propose an informal grouping, *Paniculatae*, for these two species and a second, *Pauciramosae*, for the remaining.

Among the *Pauciramosae*, a general morphological similarity in all vegetative and floral features suggests that the species of the group are closely related. They are probably of much more recent origin. The large flower of *D. grandiflora*, extending to stamens and style branches, sets this species somewhat apart, though the similarities of this streamside and open-woodland species to the forest-dwelling *D. iridioides* are many, and it is sometimes difficult to tell them apart from dried material. *Dietes butcheriana*, although distinct, appears to be a localized derivative of the less specialized *D. iridioides*, adapted to the mist forests of Natal. The localized and disjunct *D. flavida*, very difficult to distinguish from *D. iridioides*, appears also to have been derived from the more widespread *D. iridioides*, and is adapted to forest margin situations.

Morphology

ROOTSTOCK

Dietes has a thick, tough, fibrous to woody creeping rhizome which persists for several years. It bears a fan of equitant leaves at its apex. Side branches are produced from lateral buds which grow eventually to form new plants, initially grouped in a clump with the original plant.

LEAVES

The leaves of *Dietes* are, like most Iridaceae, isobilateral, and linear to ensiform, and they are arranged in a distichous fan. The leaves are thick, leathery, and fairly long-lived so that plants are evergreen. Except in *D. bicolor*, there is no discrete central vein, although several large veins run together in the lower part of the leaf. In *D. bicolor* two or more large median veins generally run very close together, simulating in appearance a midvein. Leaflike structures without a free lamina are considered bracts and are discussed in the following section.

SCAPE

The flowering stem, or scape, simply referred to in the text as the stem, is erect, fairly thick, and usually as high or higher than the leaves. The stem bears leaves on the lower nodes which decrease in size upwards. Upper nodes bear bractlike leaves that are entirely sheathing and lack a lamina. They closely resemble the spathe valves of the inflorescence, except in *D. bicolor* in which the stem bracts are smaller and often dry.

The stem is usually branched in the upper part, either forming a distinct paniclelike inflorescence as in D. robinsoniana and D. bicolor (Fig. 4) or forming

an irregular, rather lax type of inflorescence (Fig. 5). In *D. iridioides* stems are sometimes unbranched, but typically only in young individuals. At all the branch points of the stem, the subtending stem bracts are paired, a feature apparently not usual in Iridaceae, but known also in *Pilansia* (Ixioideae) and *Bobartia* (Sisyrinchioideae) (Lewis, 1954).

INFLORESCENCE

The ultimate inflorescences of *Dietes* are the terminal, so-called rhipidia typical of Iridaceae. Two opposed bracts, called spathes, enclose a several-flowered inflorescence in which individual flowers are borne one by one several days or weeks apart. The flowers are raised on a stiff pedicel which is characteristically covered with a light brown pubescence on one side. This may be difficult to see in older flowers or in fruiting plants, but is present in all species. The spathes are herbaceous but stiff in texture, with the inner longer than the outer. The apices are obtuse to emarginate and usually turn brown in mature inflorescences. Individual rhipidia may be solitary, grouped in a lax arrangement, or together form a panicle as detailed in the section dealing with the stem.

FLOWERS

The flowers are generally *Iris*-like, large, pale colored, and usually have conspicuous nectar guides at the base of the limbs of the outer tepals. The tepals are free, unguiculate, and differentiated into a larger outer and smaller inner whorl. The claws of the tepals are ascending, and the limbs spread horizontally. The claws of the outer tepals have a basal nectary and a median line of pubescence (a beard), and they are usually spotted or striped yellow to orange. The inner tepals are seldom marked, but there are conspicuous brown marks on the claws of the inner tepals of *D. grandiflora* (Fig. 8).

ANDROECIUM

The three filaments are free except in forms of *D. iridioides* and are held apart from one another. They are slender with a slightly broadened base. The anthers, held against the style branches, are extrorse, shortly tailed, and have a small apical appendage. In the southern Cape forms of *D. iridioides* the filaments are joined in the lower half and have a bulbous base. In plants occurring to the east the broadened bases of the filaments are contiguous but free.

GYNOECIUM

The ovary is large, green, and typically exserted from the spathes, though partly included in *D. robinsoniana* and sometimes in *D. bicolor*. The style, itself slender and short, divides to form three large flattened petaloid branches opposite the outer tepals. Each style branch is inclined and lies against a tepal claw. The stigma is a transverse, single or bilobed membranous structure located near the top of the style branch. The style branch bifurcates above the stigma to form a pair of petaloid appendages called crests.

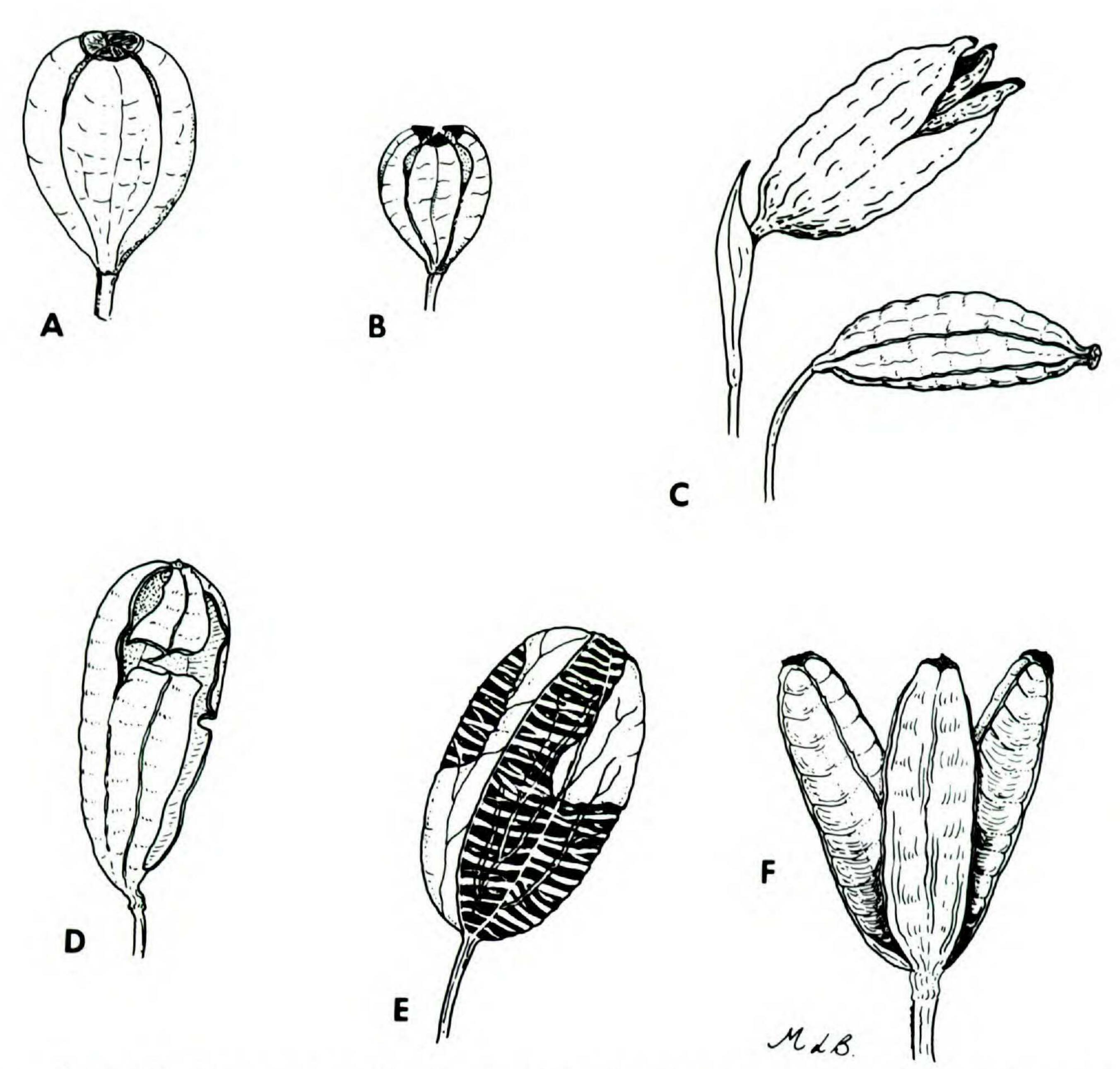


FIGURE 2. Ripe capsules of *Dietes*, all approximately life size.—A. D. robinsoniana (partially dehisced).—B. D. bicolor.—C. D. iridioides (dehiscent and indehiscent forms).—D. D. flavida.—E. D. butcheriana.—F. D. grandiflora.

FRUITS

The fruit is typically a loculicidally dehiscent capsule in *Dietes*. The degree of dehiscence varies, and fruits of *D. butcheriana* are indehiscent, while those of *D. flavida* split irregularly according to Obermeyer (1968b). The capsules are tough, thick-walled structures and are distinctive in each species (Fig. 2). In *D. robinsoniana* and *D. bicolor* the capsules are erect, globose, with a flat truncated apex and partially dehiscent from the apex to about the middle. In *D. grandiflora* and *D. iridioides* the capsules are oblong and ridged, and in the latter usually conspicuously rostrate. According to Obermeyer, the capsule of *D. grandiflora* is fully dehiscent, but in *D. iridioides* the capsules lie on the ground and decay but do not split. My own experience is contrary; I have observed *D. iridioides* in cultivation and in the field and have noted mature capsules splitting at least to the midline (Fig. 2B). Collections from the southern Cape also have partly de-

hiscent capsules. Most collections from elsewhere in Africa have capsules closed or split only near the apex, and it seems that there is some degree of variation in this character in *D. iridioides*. The capsules of *D. flavida* and *D. butcheriana* are distinctive in their smooth surface, somewhat globose rather than oblong shape, and in being pendulous (Figs. 2C–D).

SEEDS

Seeds of all species of *Dietes* are large, somewhat irregular in shape, and distinctly flattened.

SYSTEMATICS

Dietes Salisb. ex Klatt, Linnaea 34: 583. 1866, nom. cons. vs. *Naron* Medikus. TYPE SPECIES: *D. compressa* (L.f.) Klatt, nom. illeg. superf. pro *Moraea* iridioides L. = Dietes iridioides (L.) Klatt.

Naron Medikus, Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 419. 1790, nom. rej. vs. Dietes Salisb. ex Klatt. 1866. Type species: N. orientale Medikus, nom. illeg. superf. pro Moraea iridioides L. = Dietes iridioides (L.) Klatt.

Dietes Salisb., Trans. Hort. Soc. London 1: 307. 1812, nom. nudum.

Moraea Miller sensu Linnaeus, Syst. Nat., ed. 12, 2: 78. 1767; sensu Miller, Gard. Dict., ed. 8. 1768 et sensu auct., pro parte.

Iris series Dietes Salisb. ex Baker, J. Linn. Soc. Bot. 16: 147. 1878. TYPE SPECIES: I. compressa L.f. Moraea subgen. Dietes Salisb. ex Baker, Handb. Irid. 48. 1892; Fl. Cap. 6: 11. 1896. TYPE SPECIES: M. iridioides L.

Plants medium to large, perennial, evergreen, herbs. Rootstock a thick, fibrous creeping rhizome, persisting for several years. Leaves several, distichous at the apex of the rhizome, tough, leathery, equitant, linear to ensiform. Stems usually erect, bearing leaves at the lower nodes and sheathing spathelike bracts at the upper nodes; branching irregularly in the upper half or forming a distinct many-branched panicle; stem bracts paired at the branch points. Inflorescences enclosed in paired, opposed sheathing, bractlike spathes, the outer spathe smaller, the margins free to the base; flowers several per spathe, borne one at a time on stiff pedicels which are characteristically pubescent on the outer surface. Flowers large, pale colored with nectar guides at the base of the limb of the outer tepals, the claw of the outer tepal bearded to papillate in midline; tepals free to the base, the outer whorl larger, both whorls of tepals with an ascending claw and outspread limb. Filaments either free, filiform with a slightly expanded base or broad based and contiguous or united in the lower part; anthers linear, held against the style branches. Ovary green, terete, included or exserted from the spathes; styles short, dividing to form 3 branches, style branches large, flattened and petallike, bearing transverse stigma lobes on the abaxial face above which the branch bifurcates, forming paired crests. Fruit a many-seeded capsule, either indehiscent, or partly to entirely splitting along locule septa; seeds large, somewhat irregular in outline, but depressed. Basic chromosome number: x = 10.

Number of species: 6.

Distribution: forests, forest margins, and streamsides, east, central and southeast tropical Africa, coastal southern Africa, and Lord Howe Island, Australasia; Fig. 1.

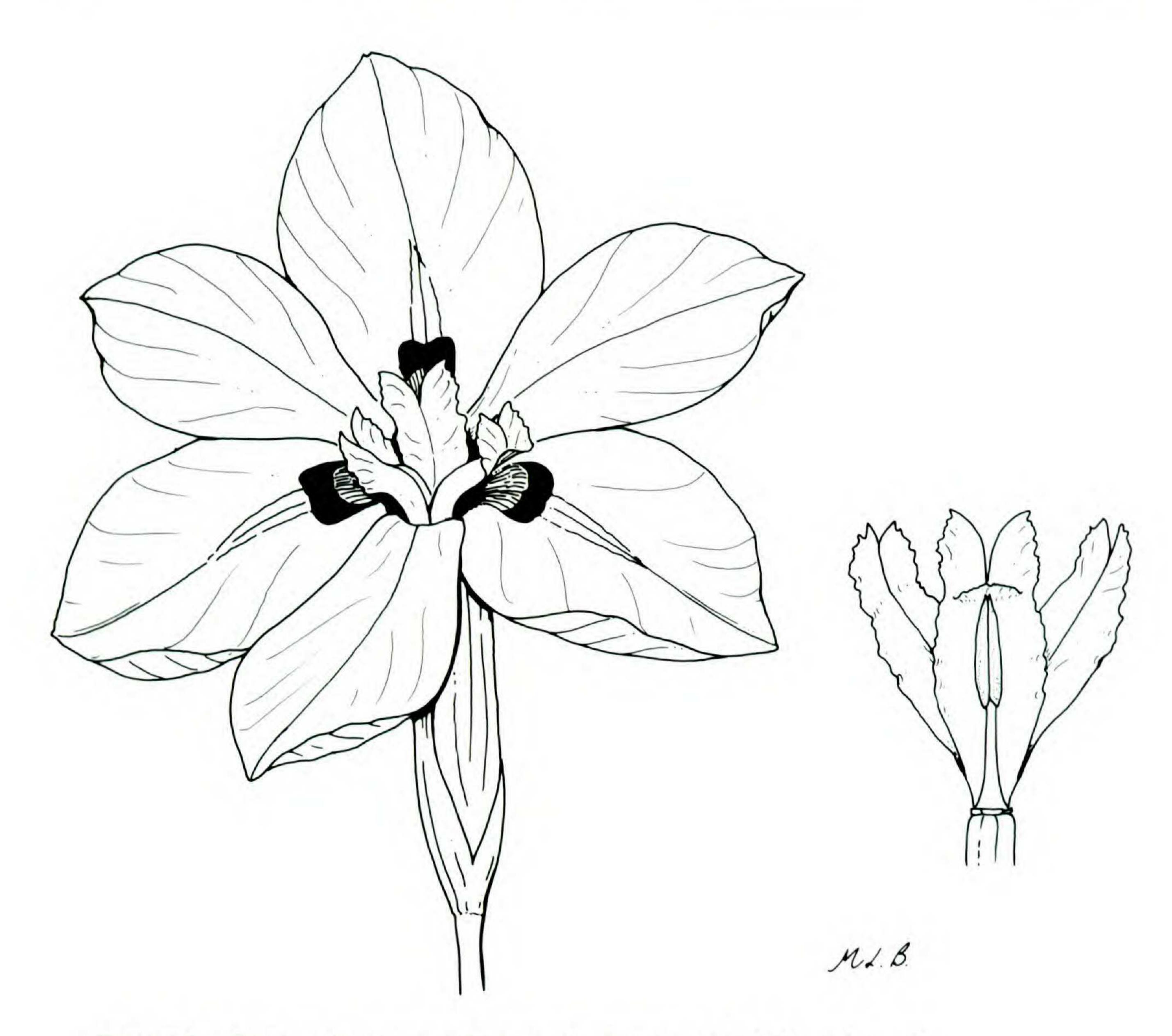


FIGURE 3. Dietes robinsoniana. Flower ×1; stamen and style branches ×2.

Artificial Key to Dietes

Leaves 30-50 mm or more at the widest point. Stem forming a regular branching panicle in the upper part; outer tepals ca. 45 mm long; stamens ca. 15 mm long _____ 1. D. robinsoniana 2'. Stem forming an irregularly branched inflorescence; outer tepals 30-32 mm long; stamens ca. 10 mm long _____ 5. D. butcheriana 1'. Leaves less than 25 mm at the widest point. Stem bracts 9-20 mm long, often brown, obviously paired _____ 2. D. bicolor Stem bracts 25-50 mm long, usually green, not obviously paired and the inner much smaller, or evidently lacking. 4. Outer tepals 45–60 mm long; style branches excluding crests 12–20 mm long; inner tepals with brown markings on the claw _____ 6. D. grandiflora 4'. Outer tepals 24-40 mm long; style branches 7-9 mm long; inner tepals not marked. 5. Flowers white with a yellow nectar guide and blue to blue-flushed style branches; capsule erect, rough walled, usually furrowed and with a conspiduous beak (filaments sometimes united in the lower half) _____ 3. D. iridioides 5'. Flowers pale yellow with an orange brown nectar guide and yellow (occasionally blue-flushed) style branches; capsule pendant, smooth walled and without

a beak (filaments always free) ----- 4. D. flavida

GROUP PANICULATAE

1. Dietes robinsoniana (F. Muell.) Klatt, Erganz. (Abh. Naturf. Ges. Halle 15: 374. 1882) 40. 1882.—Fig. 3.

Iris robinsoniana F. Muell., Fragment. Phytogr. Austral. 7: 153, 1871. TYPE: Lord Howe Island, Moore s.n. (K, holotype).Moraea robinsoniana (F. Muell.) Benth. & Muell., Fl. Austral. 6: 409. 1873.

Plants 1-1.5 m high. Leaves about as long as the inflorescences, linear-ensiform, the largest to 5 cm at the widest point. Stem erect, elliptical in section, to 15 mm thick, bearing small leaves at the lower nodes and spathelike bracts at the upper nodes; inflorescence much branched, forming the upper fifth of the stem, the nodes of the inflorescence with soft-textured, paired bracts, ranging in length from 5 cm at the lower to 2 cm at the upper nodes, the inner bract small, the outer inflated. Spathes 35-40 mm long, obtuse to emarginate, the outer ½3-½ the inner. Flowers white with orange nectar guides on the outer tepals, opening ca. 10 A.M., fading in late afternoon; outer tepals 45 mm long, the claw ca. 15 mm long, the limb horizontal, ca. 30 mm wide; inner tepals slightly smaller. Filaments to 10 mm long; anthers 5-6 mm long. Ovary ca. 8 mm long, included in the spathes; style ca. 4 mm long, the branches ca. 10 mm long, ca. 8 mm wide; crests to 5 mm long, obtuse. Capsule globose, truncate at the apex, to 30 mm long, ca. 25 mm wide, dehiscent only in the upper half. Chromosome number: 2n = 20.

Flowering time: spring and summer.

Distribution: forest and forest margins, Lord Howe Island, between Australia and New Zealand; Fig. 1.

I have noted in the earlier sections of this treatment that *Dietes robinsoniana*, the only non-African member of the genus, is correctly placed in *Dietes*. It seems to have, in fact, a combination of more unspecialized characteristics than any other species and is thus regarded as the most primitive in the genus. However, it is not altogether isolated and appears to be more closely related to the eastern South African *D. bicolor* than the latter is to the remaining African species.

2. Dietes bicolor (Steud.) Sweet ex Klatt, Linnaea 34: 584. 1863.—Fig. 4.

Moraea bicolor Steud., Nom. Bot., ed. 2, 2: 159. 1841. TYPE: South Africa, Cape, exact locality not known, illustr. in Bot. Reg. tab. 1404.

Iris bicolor Lindl., Bot. Reg. tab. 1404. 1831, hom. illeg. non Miller, Gard. Dict., ed. 8. Iris no. 13. 1768.

Dietes bicolor Sweet, Hort. Brit., ed. 3, 661. 1839, nom. inval. (Dietes nom. nudum). Dietes bicolor Spae, Ann. Gand. 2: tab. 70. 1846, nom. inval. (not accepted by author).

Plants 80–120 cm high. Leaves 50–100 cm long, linear, pale green, with a distinct, usually double central vein, 6–12 mm wide. Stem erect, bearing short leaves on the lower nodes and short paired opposite bractlike structures on the upper nodes; stem bracts herbaceous or dry and brown, 9–20 mm long, acute, the margins free to the base. Spathes herbaceous, 34–45 mm long, the outer ½–½ the inner, the margins free to the base, the apices obtuse to emarginate. Flowers yellow, usually with a dark brown nectar guide on the outer tepals, the guide sometimes lacking and the tepal claw dotted; outer tepals 35 mm long, the claw ca. 12 mm long, bearded and speckled orange, the limb horizontal, to 23 mm

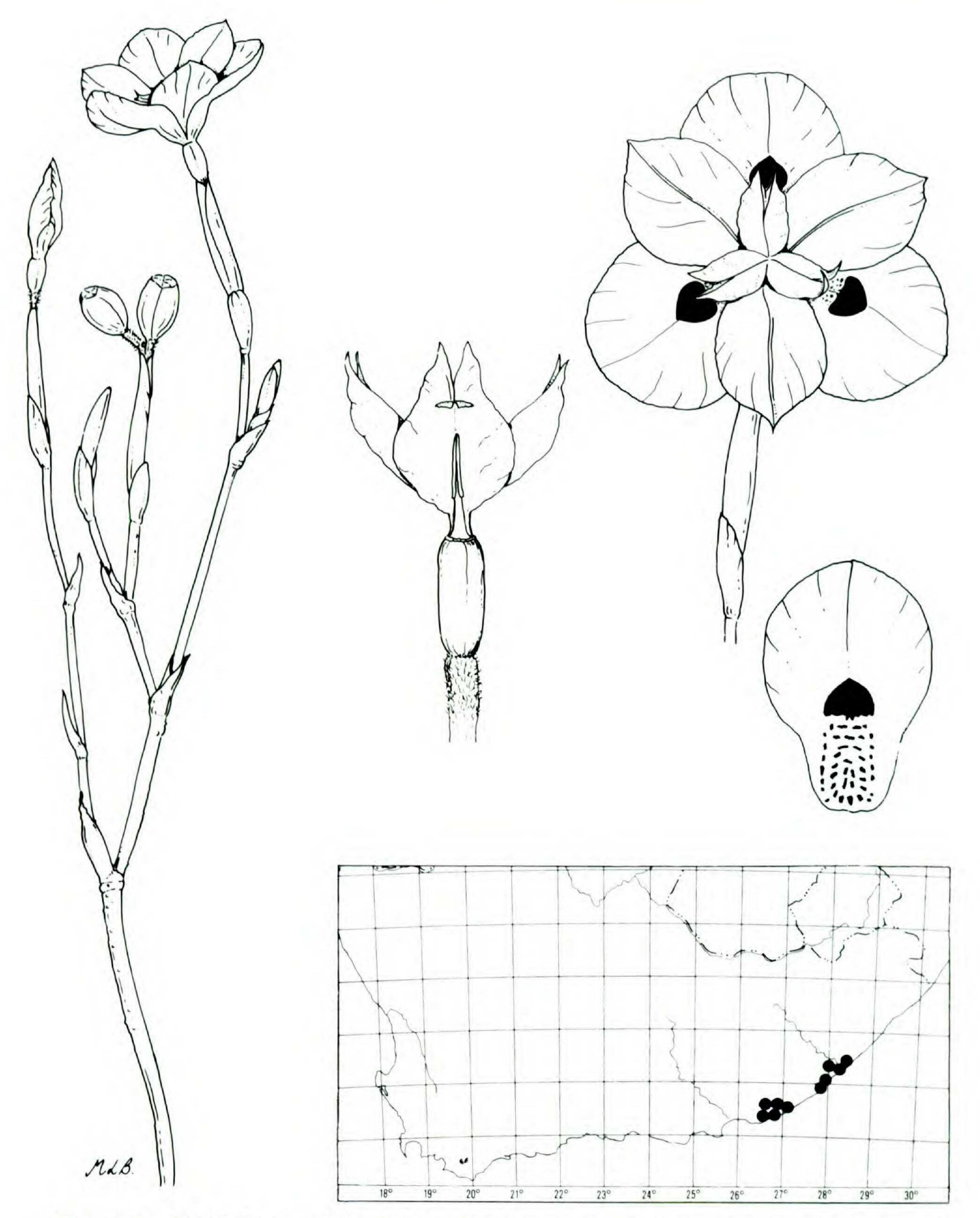


FIGURE 4. Morphology and distribution of *Dietes bicolor*. Flowering branch $\times 0.5$; flower and outer tepal $\times 1$; ovary, stamen and style branches $\times 1.5$.

wide; inner tepals to 33 mm long, ca. 18 mm wide, horizontal. Filaments 6 mm long; anthers 4–8 mm long. Ovary ca. 10 mm long; style ca. 2 mm long, the branches 8–10 mm long, to 9 mm wide; crests ca. 5 mm long. Capsule to 25 mm long, globose-truncate, dehiscing only in the upper half. Chromosome number 2n = 40.

Flowering time: spring-summer (Aug.-Feb.).

Distribution: along streams and vleis, the eastern Cape between Grahamstown and East London; Fig. 4.

Dietes bicolor, the only polyploid species of the genus, is seen as a relict, now confined to moist situations in a limited area of the eastern Cape, South Africa. It is taxonomically isolated and is almost certainly more closely related to the Lord Howe Island species, D. robinsoniana, than to any African species.

There has been some nomenclatural confusion over the authorship of the combination *Dietes bicolor* and over the original authority of the basionym. Lindley described *Iris bicolor* in 1831, but this name is illegitimate, being a later homonym. The epithet, used by Steudel in *Moraea* as *M. bicolor*, is considered valid only from this date (1841) when *M. bicolor* is considered a new name. Sweet's combination *D. bicolor* (1839) is invalid because *Dietes* was not at this time a validly described genus. Spae also used the name *D. bicolor* in 1846, but clearly did not accept this combination and instead appears to have regarded the name *Moraea bicolor* as correct for the species. *Dietes bicolor* is consequently only to be accepted from 1863 when Klatt provided a valid description for *Dietes*, and then made the combination accepted here.

Dietes bicolor is a valuable ornamental that is widely cultivated today. Plants may be very free flowering, and although each flower lasts only one day, plants usually produce flowers almost every day for months. Under unsuitable cultural conditions, D. bicolor may fail to bloom for years, while apparently healthy and producing foliage only.

3. Dietes iridioides (L.) Sweet ex Klatt, Th. Durand & Schinz, Consp. Fl. Afr. 5: 156. 1895.—Fig. 5.

Moraea iridioides L., Mant. Pl. 28. 1767. TYPE: South Africa, locality not known, cult. Chelsea Physic Gard., illustr. Miller, Fig. Pl. tab. 238, fig. 1 (lectotype).

Naron iridioideum (L.) Moench, Meth. Pl. 627. 1794.

Dietes iridioides (L.) Sweet, Hort. Brit., ed. 2, 497. 1830, nom. inval. (Dietes nom. nudum).

Naron orientale Medikus, Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 419. 1790, nom. illeg. superf. pro Moraea iridioides L.

Ferraria blanda Salisb., Prodr. 42, 1896, nom. illeg. superf. pro M. iridioides L.

Dietes iridifolia Salisb., Trans. Hort. Soc. London 1: 307. 1812, nom. inval. (Dietes nom. nudum) et superf. pro Moraea iridioides L.

Iris moraeoides Ker, Bot. Mag. sub tab. 1407. 1811, nom. nov. pro Moraea iridioides L.

1. compressa L.f., Suppl. Pl. 98. 1781; Thunb., Diss. Irid. no. 12. 1782. TYPE: South Africa, Cape, near Zeekorivier, Thunberg s.n. (Herb. Thunberg 1117 UPS, lectotype).

Dietes compressa (L.f.) Klatt, Linnaea 34: 584. 1863.

Moraea catenulata Lindl., Bot. Reg. tab. 1074. 1827. TYPE: Mauritius, R. Barclay, illustr. Bot. Reg. tab. 1074 (lectotype).

Dietes catenulata (Lindl.) Sweet ex Klatt, Linnaea 34: 585. 1863.

D. catenulata (Lindl.) Sweet, Hort. Brit., ed. 2, 497. 1830, nom. inval. (Dietes nom. nudum).

Iris crassifolia Lodd., Bot. Cab. tab. 1861. 1832, nom. nudum.

I. crassifolia G. Don, Hort. Brit., ed. 3, 661. 1839, nom. nudum.

Moraea vegeta L. sensu Miller, Gard. Dict., ed. 8. 1768.

Dietes vegeta (L.) N. E. Br. sensu N. E. Br., J. Linn. Soc. Bot. 48: 36. 1928. = M. vegeta L.

Moraea iridioides var. prolongata Baker, Fl. Cap. 6: 26. 1896. TYPE: not cited but probably Natal, Inanda, Wood 1341 (K).

Dietes prolongata (Baker) N. E. Br., J. Linn. Soc. Bot. 48: 37. 1928.

Dietes prolongata var. galpinii N. E. Br., J. Linn. Soc. Bot. 48: 37. 1928. TYPE: South Africa, Transvaal, near Barberton, Galpin 1206 (K, lectotype).



FIGURE 5. Morphology and distribution of *Dietes iridioides*. Fruiting branch $\times 0.5$; flower $\times 1$; ovary, stamen and style branches $\times 1.5$.

Plants (15-)30-60 cm high. Leaves 25-40(-60) mm long, 6-15(-25) mm wide, linear-ensiform. Stem bearing short leaves below, and sheathing, bractlike leaves above, irregularly branching; stem bracts 25-30 mm long, often dry and brownish; old inflorescences often producing long stolons which bear a fan of leaves distally that eventually root. Spathes 35-50(-55) mm long, the outer ca. ½ the inner, obtuse-emarginate at the apex. Flowers white with yellow nectar guides on the outer tepals, the claws of the outer and often the inner tepals orange dotted, the style branches blue or white, flushed with blue; outer tepals 24-35 mm long, the claw ca. 16 mm long, heavily ciliate in midline, papillate, the limb spreading to recurved, 12-16 mm wide; inner tepals 24-28 mm long, 9-12 mm wide, spreading-recurved. Filaments 5-9 mm long, free or united or contiguous in the lower 3 mm; anthers 3-6 mm long. Ovary 8-15 mm long, lightly ridged; style 2-3 mm long, the branches 7-9 mm long, 4-6 mm wide; crests ca. 5 mm long. Capsule ovoid-cylindric, usually rostrate, 20-30 mm long, 14 mm in diameter. Chromosome number: 2n = 20.

Flowering time: sporadic during spring and summer, blooming earliest in areas of winter rainfall.

Distribution: evergreen forests, from the southern Cape near Riviersonderend throughout eastern southern Africa and northwards through Rhodesia, Malawi, Zambia, eastern Zaire, Tanzania, Uganda, to Kenya; Fig. 5.

Dietes iridioides is the most widespread and common species of the genus, extending almost from the southern tip of Africa to Kenya. It is easy to distinguish from related species by its relatively small white flower with violet style branches, and its rostrate, cylindrical capsule, which is frequently indehiscent. Following Obermeyer (1968a), I include as synonyms D. prolongata, a species recognized by N. E. Brown, as well as its variety, var. galpinii. The name D. prolongata was given to stolon-producing plants of D. vegeta, said to have unmarked outer petals. Stolon production is common in D. iridioides and may occur on any plant with old inflorescences.

Dietes iridioides was for several years known as D. vegeta (L.) N. E. Brown, following Brown's (1928) erroneous conclusion that Linnaeus's Moraea vegeta (1762) was to be typified by the illustration published in Miller's Figures of Plants (tab. 238, fig. 1), which is the type of Moraea iridioides (and thus of D. iridioides (1767). The reasons for Brown's error and the restoration of the name D. iridioides for the species have been described at length elsewhere (Barnard & Goldblatt, 1975). Moraea vegeta is the type species of Moraea and is currently regarded as the correct name for the Cape species also sometimes known as M. tristis (L.f.) Ker (Goldblatt, 1976).

There is an interesting pattern of variation in *D. iridioides*. Plants in the southern part of its range, in the southern Cape as far east as the Humansdorp district, have filaments united in the lower half. The filament column is distinctively swollen and bulbous towards the base. North and east of these populations, in the eastern Cape, essentially a summer rainfall area, plants have filaments with a similar bulbous base, but the individual filaments are free, but contiguous. I have seen few plants from the rest of the range, but other reports indicate that the filaments are narrower, with only slightly expanded bases, and they are en-

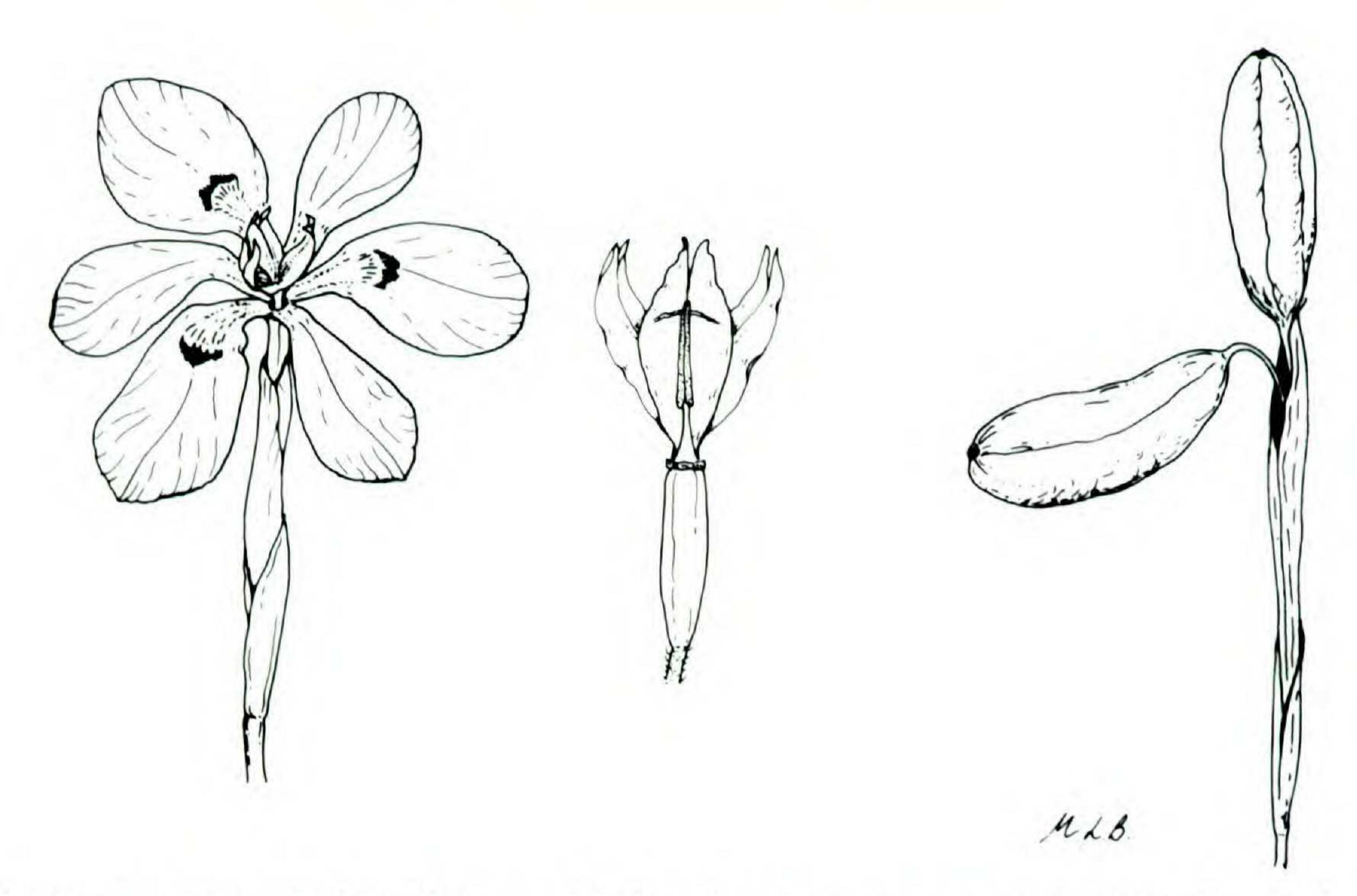


FIGURE 6. Dietes flavida. Flower and fruits ×1; ovary, stamen and style branches ×1.5.

tirely free. The pattern is apparently continuous. There seems no need to express this situation in a formal taxonomic way, but the condition of united filaments in the southern Cape plants indicates that they comprise a clearly recognizable form of *D. iridioides*.

4. Dietes flavida Obermeyer, Fl. Pl. Africa 149: tab. 1488. 1967. TYPE: South Africa, Natal, Jozini Dam, Admiraal 5293 (PRE, holotype).—Fig. 6.

Plants 50–70 cm high. Leaves 30–50 cm long, linear-ensiform, 15–22 mm wide. Stem bearing leaves below and reduced sheathing spathelike leaves above; branching irregularly; stem bracts 30–50 mm long. Spathes (40–)45–50 mm long, the outer ca. ½ inner, the apices obtuse to emarginate. Flowers pale yellow, with brown nectar guides on the outer tepals and spotted on the claw; outer tepals 30–40 mm long, the claw ca. 15 mm long, the limb horizontal, 15–17 mm wide; inner tepals smaller, to 38 mm long. Filaments 4–6 mm long, broadened at the base; anthers 5–6 mm. Ovary 10–14 mm long; style 2–3 mm long, the branches ca. 8 mm long, 3–4 mm wide; crests 5–10 mm, acute. Capsule ovoid, pendulous, smooth, 30–35 mm long, ca. 12 mm in diameter, dehiscing irregularly. Chromosome number: 2n = 20.

Flowering time: sporadically during the summer months.

Distribution: along forest margins and lightly shaded areas, Lebombo Mountains of northern Natal and Swaziland, also recorded from the Baviaans Kloof Mountains in the eastern Cape; Fig. 7.

Dietes flavida is closely related to the widespread D. iridioides, and is easily confused with this species. When living the two are readily distinguished by flower color as well as leaf characteristics. Dietes flavida has cream to yellow

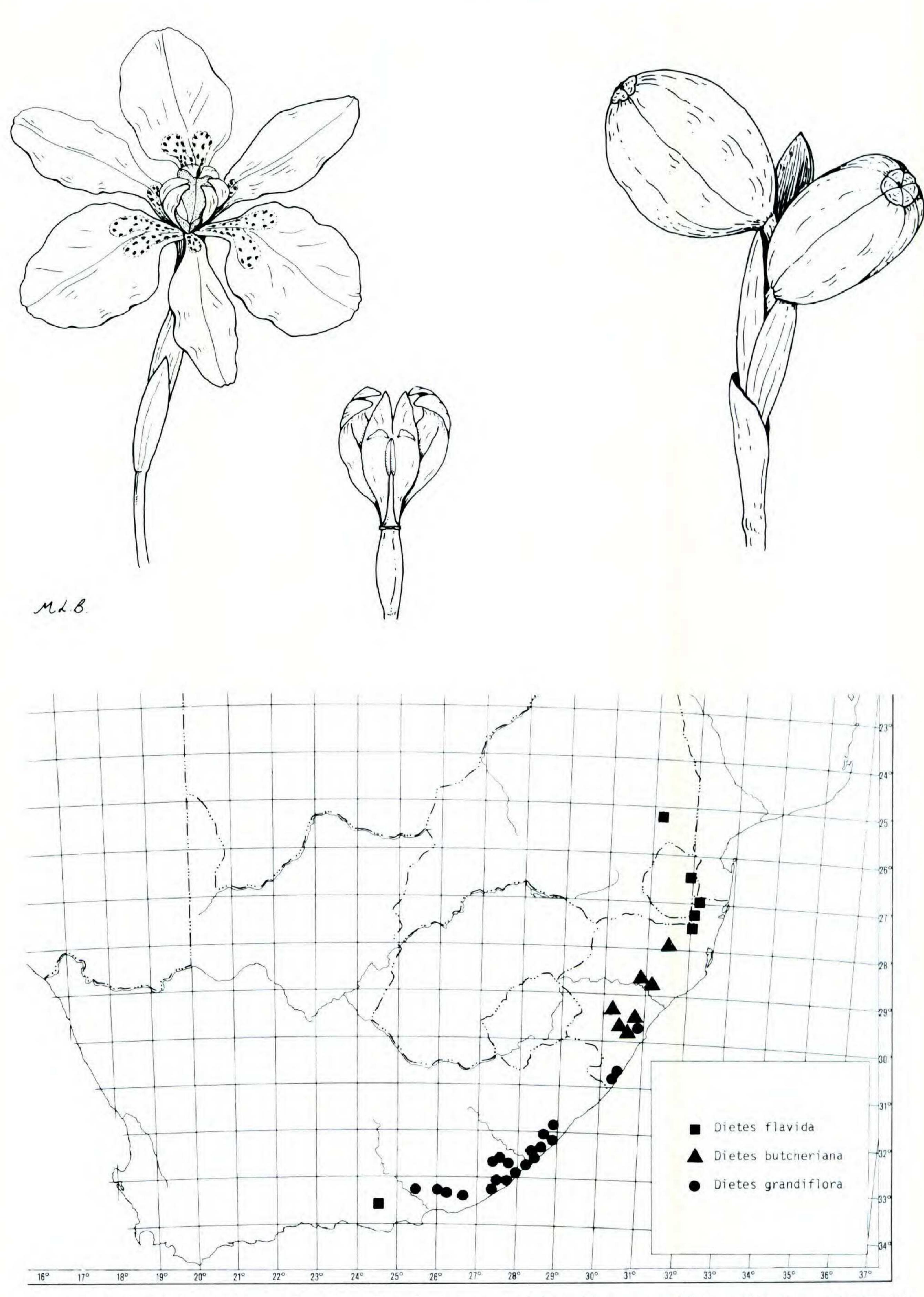


FIGURE 7. Morphology of *Dietes butcheriana*, and distribution of *D. butcheriana*, *D. flavida* and *D. grandiflora*. Flower and fruits $\times 1$; ovary, stamen and style branches $\times 1.5$.

flowers with brown-spotted nectar guides, the style branches are usually also cream or rarely very lightly flushed with purple, and the leaves have a grayish waxy covering. *Dietes iridioides*, in contrast, has white flowers with style branches conspicuously blue-purple flushed, and dark green leaves. When dry these

characters are lost, and fruits are needed for accurate determination. The fruits of *D. flavida* are oblong-ovoid, smooth, pendulous, and dehisce irregularly instead of along the carpel sutures. The fruits of *D. iridioides* are typically oblong and distinctly beaked, have a somewhat fissured surface, and are either indehiscent, or they split along the carpel sutures from the apex downwards for some distance.

Dietes flavida is characteristic of more open sites than the shade-loving D. iridioides, and it is reported to occur along forest edges, on cliffs, and along streams. When described by Obermeyer in 1967, D. flavida was thought to be restricted to the southern Lebombo Mountains in Natal and Swaziland. It has now been collected by R. D. Bayliss in the Baviaans Kloof Mountains of the southeastern Cape. This range disjunction is remarkable. Further collecting may bring to light some stations between these two extremes, but it is clear that this is nevertheless a true disjunction.

5. Dietes butcheriana Gerstner, J. S. African Bot. 9: 149. 1943. TYPES: South Africa, Natal, Nkandla Forest, Zululand, Gerstner 601 (NH, lectotype); Gerstner 4159 (NH, syntype); Obermeyer, Fl. Pl. Africa 149: tab. 1487. 1967.—Fig. 7.

Plants 50–120 cm high. Leaves larger than the stem, to 100(–120) cm long, ensiform, 30–48 mm wide. Stem thick, often somewhat flexuous, 50–60 cm long, with small leaves on the lower nodes and sheathing spathelike bracts on the upper nodes; stem bracts 30–60 mm long; branches relatively short. Spathes 45–60 mm long, the outer ca. ½ the inner, acute, obtuse or emarginate at the apex. Flowers white with yellow nectar guides on the outer tepals, the claws of the inner and outer tepals speckled orange, the style branches white; outer tepals 30–35 mm long, the claw 12 mm long, bearded, the limb spreading, 15–20 mm wide; inner tepals 25–35 mm long, to 12 mm wide, the limb spreading. Filaments 6 mm long; anthers 4–4.5 mm long. Ovary ca. 10 mm long; style ca. 3 mm long, the branches 8–9 mm long, 6–8 mm wide; crests 7–10 mm long. Capsule subglobose, 25–35 mm long, 20 mm in diameter, subpendulous, indehiscent, smooth when ripe. Chromosome number: 2n = 20.

Flowering time: sporadic, mainly spring and summer.

Distribution: in deep shade, in mist-belt forests, Natal and Zululand; Fig. 7.

Dietes butcheriana, a Natal endemic of moist forest areas, is closely related to D. iridioides and may be regarded as a specialized derivative of this widespread African species. Dietes butcheriana can easily be distinguished by its very broad leaves, ca. 30–50 cm wide, white flowers without purple or blue-flushed style branches, and globose, smooth, indehiscent capsules.

6. Dietes grandiflora N. E. Br., J. Linn. Soc. Bot. 48: 35. 1928. TYPE: South Africa, Cape, Kentani Div., *Pegler 484* (K, lectotype; BOL, isolectotype).—Fig. 8.

Plants tall, 1-1.5 m high. Leaves 75-100 mm long, linear, 10-15(-20) mm wide. Stem branched irregularly, bearing short leaves at the lower nodes and spathelike bracts from the upper nodes; stem bracts 25-50 mm long, entirely

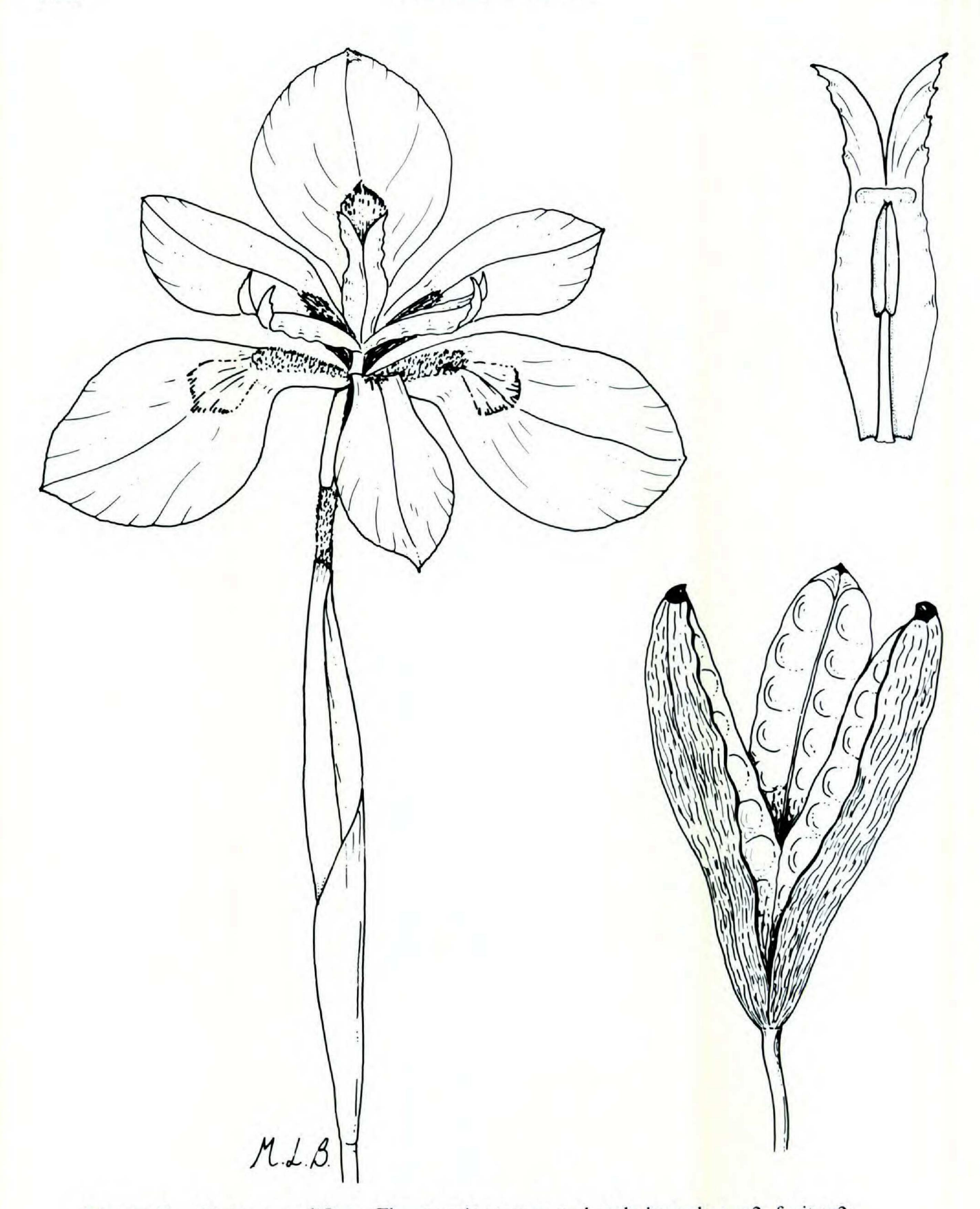


FIGURE 8. Dietes grandiflora. Flower ×1; stamen and style branches ×2; fruit ×2.

sheathing, herbaceous, the apices obtuse apiculate. Spathes 50–80 mm long, the outer about ½ the inner, the margins free to the base, the apices obtuse or emarginate. Flowers white with yellow nectar guides and a yellow beard on the outer tepals, the inner tepals marked dark brown towards the base, the style branches pale mauve; outer tepals 45–60 mm long, the claw 20–26 mm long, with a dense yellow beard down the midline, the limb horizontal to recurved, 25–35 mm wide; inner tepals (36–)40–45 mm long, to 25 mm wide, the limb spread

horizontally. Filaments 10–13 mm long, tapering from a broad base to the apex, contiguous at the base; anthers 7–10 mm long. Ovary 13–16 mm long; style ca. 5 mm long, the branches 12–20 mm long, 6–8 mm wide; crests 12–15 mm long, erect. Capsule 28-45(-50) mm long, ridged and furrowed vertically, cylindrical. Chromosome number 2n = 20.

Flowering time: sporadic, during spring and summer.

Distribution: forest margins and especially along streams, the Eastern Cape from King William's Town through the Transkei to Natal; Fig. 7.

Dietes grandiflora stands out as the largest-flowered species of the genus. It is related to the more widespread D. iridioides but is easily distinguishable by its height and large flowers, which last three days in contrast to those of D. iridioides which last a single day. The flowers of D. grandiflora are conspicuously marked with a heavy yellow beard on the claws of the outer tepals, while the inner tepals have dark brown markings. This species is widely cultivated in areas of tropical to subtropical climates, and it will stand light frost. Once established, the plants are extremely persistent even when completely neglected. However, more and larger flowers and a longer flowering season reward those who give the plant better care.

LITERATURE CITED

- BAKER, J. G. 1896. Irideae. In W. T. Thiselton-Dyer (editor), Flora Capensis 6: 9-171. Reeve & Co., London.
- ——. 1898. Irideae. In W. T. Thiselton-Dyer (editor), Flora of Tropical Africa 7: 337-376. Reeve & Co., London.
- Banerjee, J. & A. K. Sharma. 1971. A cytotaxonomical analysis of several genera of the family Iridaceae. Pl. Sci. 3: 14-29.
- BARNARD, T. T. & P. GOLDBLATT. 1975. A reappraisal of the application of specific epithets of the type species of *Moraea* and *Dietes* (Iridaceae). Taxon 24: 125-131.
- Brown, N. E. 1928. The Iridaceae of Thunberg's Herbarium. J. Linn. Soc. Bot. 48: 34-42.
- BRUMMITT, R. K. 1978. Report of the committee for Spermatophyta, 20. Taxon 27: 285-289.
- CHIMPHAMBA, B. B. 1974. Karyotype analysis in *Moraea* and *Dietes*. Cytologia 39: 525-529. Gerstner, F. J. 1943. *Dietes butcheriana* Gerstner, J. S. African Bot. 9: 149-151.
- GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37: 317-460.
- ——. 1973. Proposal for the conservation of the generic name *Dietes* Salisb. (1812) against *Naron* Medik. (1796) (Iridaceae). Taxon 22: 504–505.
- ——. 1976. A revision of *Moraea* (Iridaceae) in the winter rainfall region of southern Africa. Ann. Missouri Bot. Gard. 63: 657–786.
- ——. 1978. A contribution to cytology in Cornales. Ann. Missouri Bot. Gard. 65: 650-655.
- ——. 1979. Preliminary cytology of Australasian Iridaceae. Ann. Missouri Bot. Gard. 66: 851-855.
- KLATT, F. W. 1866. Revisio Iridearum: Dietes. Linnaea 34: 583-586.
- ——. 1882. Erganzungen und Berichtigungen zu Baker's Systema Iridacearum. Halle.
- ——. 1895. Irideae. In Th. Durand & H. Schinz (editors), Conspectus Florae Africanae 5: 143–230. Charles Vande Weghe, Bruxelles.
- Lewis, G. J. 1954. Some aspects of the morphology, phylogeny and taxonomy of the South African Iridaceae. Ann. S. African Mus. 40: 15-113.
- MEDIKUS, F. C. 1790. Naron. Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 419.
- Моемсн, С. 1794. Methodus Plantas. Marburg, Libraria Academiae.
- OBERMEYER, A. A. 1967a. Dietes butcheriana. Fl. Pl. Africa 38: tab. 1487.
- 1967b. Dietes flavida. Fl. Pl. Africa 38: tab. 1488.
- 1968a. Dietes vegeta. Fl. Pl. Africa 39: tab. 1524.
- _____. 1968b. Dietes bicolor. Fl. Pl. Africa 39: tab. 1525.
- RAVEN, P. H. & D. I. AXELROD. 1974. Patterns of angiosperm distribution in the light of continental drift. Ann. Missouri Bot. Gard. 61: 539-673.

- RILEY, H. P. 1962. Chromosome studies in some South African monocotyledons. Canad. J. Genet. Cytol. 4: 50-55.
- SAKAI, B. 1952. Zytologische Untersuchungen bei Iridaceae I. Über die Karyotypen verschiedener Arten der Unterfamilie Iridioideae. Cytologia 17: 104–111.
- Salisbury, R. A. 1812. On the cultivation of rare plants, especially such as have been introduced since the death of Mr. Philip Miller. Trans. Hort. Soc. London 1: 261–360.
- SHARMA, A. K. & A. SHARMA. 1960. Cytology of some members of the family Iridaceae. Cytologia 26: 274–285.
- SPAE, D. 1846. Dietes bicolor. Ann. Soc. Roy. Agric. Gand 2: 233-234.
- 1852. Moraea bicolor. Fl. Serres Jard. Eur., sér. 1, 7: tab. 744.
- SWEET, R. 1830. Hortus Britannicus. Ed. 2. Ridgeway, London.
- —. 1839. Hortus Britannicus. Ed. 3. Ridgeway, London.